

COMPARATIVE OBSERVATIONS ON THE PLACENTA AND FOETAL NUTRITION IN ELASMOBRANCHS AND MAMMALS

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(With two plates)

CONTENTS

1. INTRODUCTION	...	...	...	...	...	...	831
2. TABLE SHOWING THE NATURE OF PLACENTAE IN BOMBAY ELASMOBRANCHS	...	...	...	...	...	...	832
3. A COMPARATIVE ACCOUNT OF THE SELACHIAN AND MAMMALIAN PLACENTAE	...	...	...	...	...	...	832
4. EMBRYONIC ALIMENTATION IN ELASMOBRANCHS	...	...	...	...	...	...	835
5. SUMMARY	...	...	...	...	...	...	839
6. REFERENCES	...	...	...	...	...	...	840

INTRODUCTION

Accounts of the anatomy and histology of the placenta in elasmobranchs are scarcely comprehensive and certainly too scattered to permit of a clear and comprehensive picture of the complex nutritional processes that characterise the foetal life of this group of fishes. The present paper is a generalised discussion of the phenomenon of placenta in elasmobranchs, based principally on the author's study of over a dozen placental forms in Bombay, the detailed observations on which have been presented before in a series of papers published elsewhere (*vide* References).

The subject matter has been presented in the form of a comparison with the mammalian placenta, the concept of comparison being the most natural one while dealing with an organ performing the same essential function in two classes of vertebrates so widely separated in the ladder of evolution. In the light of this comparison an attempt is made to interpret the mechanism of action of the yolk-sac and the yolk-sac placenta, the early or late formation of which among elasmobranchs seems to be influenced by the initial quantity of yolk in the mature ovum.

Finally, a discussion on the influence of the appendicula on embryonic alimentation and their possible relationship to the mature ovum and the placenta has also been added, since these structures play no less important a role in the foetal nutrition in some of the species of this group.

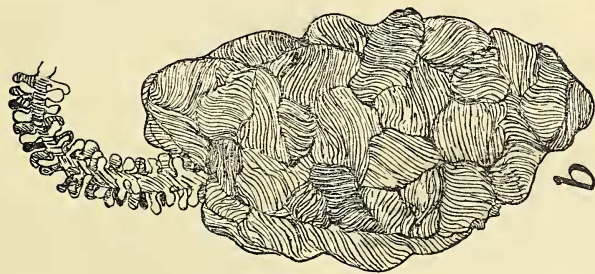
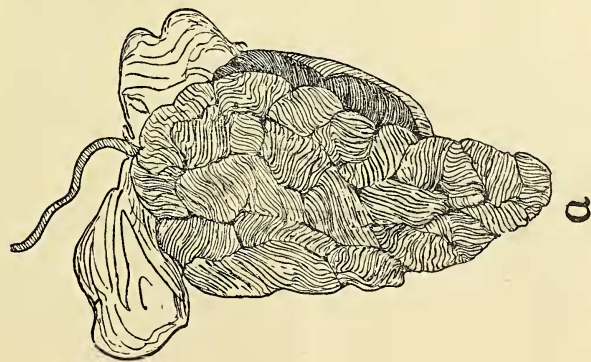
TABLE SHOWING THE NATURE OF PLACENTAE AND APPENDICULA IN SOME OF THE ELASMOBRANCHS OF THE BOMBAY WATERS

Name of species	Nature of a placenta		Nature of appendicula
	Morphological	Histological	
1. <i>Scoliodon sorrakowah</i>	Simple, contact type.	Haemo-epithelio-chorial.	Very long, prominent strap-shaped structures.
2. <i>Scoliodon palasorrah</i>	Firm, interdigitating type with folding over the entire face—Entire.	Epithelio-chorial.	Delicate, thread-like and much branched.
3. <i>Scoliodon walbeehmi...</i>	"	"	Short, " irregular
4. <i>Scoliodon acutus</i> ...	"	"	outpushings of the placental cord sheath.
5. <i>Aprionodon acutidens</i>	"	"	No appendicula.
6. <i>Hypoprion macloiti</i> ...	"	"	"
7. <i>Carcharinus limbatus</i>	"	"	"
8. <i>C. melanopterus</i> ...	Firm, interdigitating type with folding only basally—Discoid.	"	"
9. <i>C. sorrah</i> ...	"	"	"
10. <i>C. temminckii</i> ...	"	"	"
11. <i>C. menisorrah</i> ...	Entire	"	"
12. <i>Hemigaleus balfouri...</i>	"	"	Rather short, delicate and much-branched threads.
13. <i>Hemipristis elongatus</i>	"	"	Broad, vascular frills of the placental cord sheath.
14. <i>Sphyrna blochii</i> ...	"	"	Gelatinous, lobulated structures sometimes bi-lobed and tri-lobed.
15. <i>S. zygaena</i> ...	"	"	Flattened, obovate leaf-like flaps of the placental cord sheath.

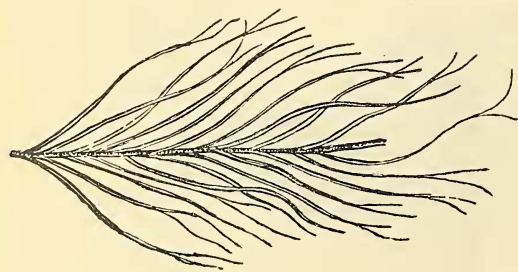
A COMPARATIVE ACCOUNT OF SELACHIAN AND MAMMALIAN PLACENTAE

1. The placenta in elasmobranchs is a simple yolk-sac placenta as distinguished from the yolk-sac placenta found in some of the primitive mammals such as *Opposum* and *Dasyurus*, in which this organ is, in part at least, composed of the foetal membranes—amnion and chorion, characteristic of the amniota. The selachian yolk-sac placenta is thus, anatomically not comparable either to the allanto-chorionic or to the truly chorionic placenta of the higher mammals.

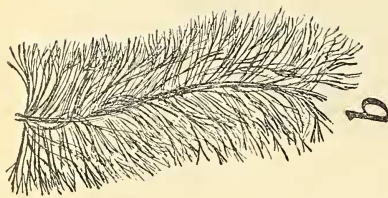
2. In all the placental elasmobranchs examined by me, with the solitary exception of *Scoliodon sorrakowah* (*vide* Table), the wall of the yolk-sac becomes excessively folded with the gradual consumption



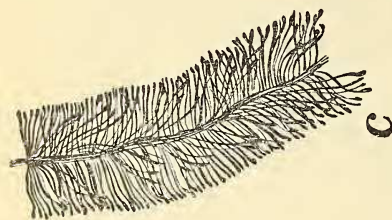
Foetal placentae in Bombay elasmobranchs. (a) entire placenta (*Hypoprius macdoti*); (b) entire placenta (*Sphyrna blochii*); (c) discoid placenta (*Carcharinus temminckii*).



a



b



c



d



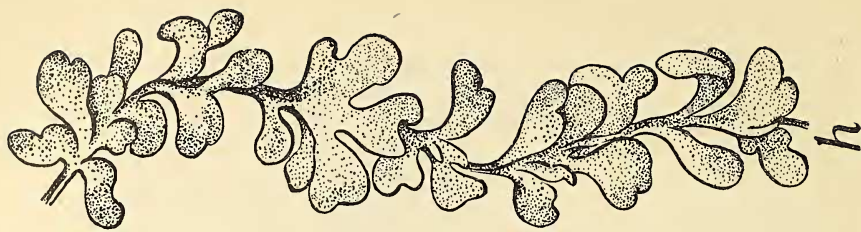
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of the yolk and the folds are highly vascularised by the placental vessels. The wrinkled and frayed yolk-sac folds fit firmly on the furrows between the vascular villi of the maternal trophonema, which constitutes the maternal portion of the placenta. Both the foetal and the maternal parts are held together by a firm inter-digitating arrangement which represents the fourth and final stage of contact in Ercolani's (as quoted from Needham, 1931) classification of the selachian placentae.

A similar inter-digitating contact between the foetal and maternal tissues also exists in placenta of Ungulates.

3. Two morphological varieties of the selachian foetal placenta described above may be said to exist among the various elasmobranchs examined by me. They are: (i) the discoid placenta (Text-fig. 1, c) and (ii) the entire placenta (Text-fig. 1, a & b). This nomenclature is adopted purely on the basis of the extent of folding undergone by the wall of the original yolk-sac. The folding in the 'discoid' placenta is confined only to the basal region of the yolk-sac where it forms a thick and spongy mass, roofed over by a free, unwrinkled proximal portion of the yolk-sac wall, while the process of wrinkling in the 'entire' placenta extends all over the yolk-sac wall with very little or no free portion at all.

In mammals, the extent of the chorionic villi on the placenta forms the basis of placental classification, there being such morphological varieties as diffuse, cotyledonary, zonary and discoid.

4. In the inter-digitating type of the selachian placenta described above, the foetal and the maternal tissues, at birth, are merely withdrawn from each other like fingers from a glove. There is no shedding of the maternal tissue. These may, therefore, be described as corresponding to the adeciduate placentae of the Ungulata.

5. The secretion of a nutritive lymphoid exudate from the uterine mucous membrane in primitive mammals and of the 'uterine milk' in ruminants and their absorption by the foetal tissue are, in a way, comparable to the nutritive uterine secretions in elasmobranchs in general and their absorption by such embryonic structures as yolk-sacs, branchial filaments, appendicula and the embryonic body generally. These latter secretions have been designated by Needham (1942) as 'histotrophe'. As in mammals, histotrophe has been observed by me in our elasmobranchs to be more copious when a placenta is either absent, as in some of the viviparous Batoids such as *Dasyatis*, *Pteroplatea*, *Aetobatus*, *Mobula*, etc. (aplacental viviparity) or is present but is poor in functional efficiency as in *S. sorrakowah*.

It would be relevant to refer at this stage to Ranzi's (as quoted by Needham, 1942) work on foetal nutrition in some of the European elasmobranchs. He made quantitative determinations of the embryonic development in oviparous (*Scyllium canicula*), ovo-viviparous¹ (*Trygon*, *Myliobatis*, *Acanthias*, *Centrophorus* etc.) and viviparous forms and his work tends to show that the histotrophic form of

¹ Ranzi has used the term (ovo-viviparous) to denote non-placental viviparous elasmobranchs, and the term (viviparous) to denote placental forms.

alimentation is even more efficient than the placental form as evidenced in *Mustelus laevis*, the type specimen of selachian placental viviparity (epithelio-chorial placenta). Ranzi has, however, pointed out that the absorption of yolk and the speed of embryonic development are greater in the placental *M. laevis* than in the non-placental, ovo-viviparous forms *M. vulgaris* and *M. antarcticus*.

6. The histology of the placenta in *Scoliodon palasorrah* which may be regarded as the type of the discoid and entire placentae referred to above, has been admirably described by Mahadevan (1940). According to her a number of tissue layers intervene between the foetal and the maternal blood streams. These are, from the maternal to the foetal side, (i) endothelium of the maternal blood capillaries in the villi of the trophonema, (ii) the uterine mesoblast, (iii) uterine epithelium covering the villi, (iv) yolk-sac ectoderm, (v) yolk-sac mesoderm and (vi) endothelium of the yolk-sac blood-capillaries.¹ In the most advanced stages of the placenta, the various layers show a tendency to attenuation, so as to bring about a closer apposition of the maternal and foetal blood-streams. On a histological basis of tissue relationship, the above type of placenta in mammals is described by Otto Grosser (as quoted by Needham, 1931) as of the epithelio-chorial variety in which six tissue layers similar to those mentioned above intervene between the foetal and maternal bloods. The barriers between the two bloods in this variety of placenta are more numerous than in the other histological varieties such as the syndesmochorial, endothelio-chorial and haemo-chorial described by Grosser and consequently, the efficiency in the exchange of materials is correspondingly lower than those of the others. In the evolution of mammalian placentae, the epithelio-chorial variety is regarded as the most primitive and the haemo-chorial, the most highly evolved.

7. Unlike the mammalian placentae, a selachian placenta [except that of *S. sorrakowah*, vide (8) below], is usually formed at a fairly advanced stage of embryonic development when the various foetal organs and systems have already been formed and have presumably taken up their respective functions also. The intimate contact between the highly vascularised foetal and maternal tissues in this placenta leads one to the view that active diffusion is set up between the foetal and maternal circulation, that a vigorous transference of nutritive materials takes place from the maternal to the foetal blood, and vice-versa, a flow of excretory products in the opposite direction. (vide *infra*).

8. The placenta in *Scoliodon sorrakowah* is unique among the elasmobranchs thus far studied by me. The initial quantity of yolk in the mature ovum of this species being very small, the maternal organism is called upon to exert to the utmost, and very early too, in the nurture of the embryo. The maternal portion of the placenta takes the form of a very prominent, elongated process of the uterine mucosa—the trophonema, a highly glandular organ (Setna &

¹ According to my anatomical findings, there exists between (iii) and (iv) above, the thin and hyaline, non-cellular layer of the shell-membrane which intervenes between the foetal and maternal tissues of all the entire and discoid placentae examined by me with the solitary exception of that of *Hemigaleus balfouri*.

Sarangdhar, *Rec. Ind. Mus.*, Vol. 46, 1949). The actual contact between the foetal yolk-sac and the maternal trophonema is, however, one of mere apposition (only the second stage in Ercolani's classification of selachian placentae) and not of an intimate inter-digitation as in the other placenta elasmobranchs. Histologically, too, this placenta is unique in that free maternal blood is extravasated within the trophonema to supply nourishment, in part at least, to the growing embryo. In order to describe this tissue relationship between the mother and the foetus, we have had to create a new histological category, viz.—the 'haemo-epithelio-chorial' variety, a nomenclature in which the syllable 'haemo' stands for free maternal blood 'epithelio' for the 'maternal trophoblast' and the syllable 'chorial' for the foetal tissue, though however, it may be repeated that the latter tissue in fishes is *not a true chorion*. Curiously enough, this placenta displays close structural convergence towards that most highly evolved placenta in higher mammals, including man—the haemo-chorial variety in which, too, free maternal blood ('haemo') is extravasated for the direct nurture of the foetal tissue—the chorionic trophoblast. The significant difference between the two above-mentioned types of placentae is, however, at once apparent by the fact that while the maternal blood in mammals bathes a foetal trophoblast, that in *S. sorrakowah* bathes a maternal one—a difference which appears to be only in keeping with the view that the foetal tissue in such primitive vertebrates as fishes is not endowed with the higher physiological faculties of a true avian or mammalian trophoblast—faculties such as phagocytosis, selective absorption, elaboration and synthesis etc. which the ceaseless forces of evolution have so conspicuously bestowed upon the succeeding ascending classes of vertebrates, thus rendering their foetal tissue more and more independent of the maternal intervention.

Being structurally comparable to the most highly evolved haemo-chorial placenta of mammals and man, one may perhaps be led to suppose that functionally too, the placenta in *S. sorrakowah* is more highly evolved than the other variety among the elasmobranchs. The predominantly histotrophic condition of this placenta does not, however, warrant such a supposition, for, as already pointed by us (*loc. cit.*) the placenta in *S. sorrakowah* is functionally more a gland than a haemotrophic organ. Judging thus, (and this would be the only basis of consideration in placental nutrition) one must say that the placenta in *S. sorrakowah* is low in evolution (functional efficiency) in spite of the fact that it displays a surprising structural convergence towards the most highly evolved placenta among that highest class of vertebrata—the mammals.

EMBRYONIC ALIMENTATION IN ELASMOBRANCHS

Yolk is the complex food material prepared and stored in the ovum by the maternal organism for the use of the developing embryo. It consists of the highly specialised and elaborated organic and inorganic substances necessary for the building up of the embryonic tissues and organs, so that the embryonic cells are, in the initial stages at least, spared the task of elaboration and synthesis. In the ovum, yolk is tightly packed in the form of more or less solid

granules or plates, but after the fertilization stimulus and the commencement of embryonic development, it is emulsified and liquified so as to become more mobile for distribution. The task of 'rendering the yolk-plates fit for absorption by blood' is, according to Beard (1896), performed, upto the critical stage¹, by the yolk-merocytes, so that the yolk may readily diffuse through the walls of the yolk-sac and the blood capillaries interspersed in its mesoblastic tissue. These merocytes are, according to the author, concentrated in the region of the yolk-sac blood-capillaries and their action on the yolk is to 'emulsify or prepare it for digestion and absorption'. This statement of Beard's needs, in my opinion, further elucidation so as to accord with the known bio-chemical principles of digestion and absorption.

Emulsification is a process by which a change is brought about only in the physical state of the yolk-granules and according to the modern concepts of the phenomenon of diffusion only crystalloids and gases are diffusible but not the colloids. Hence, even after the emulsification of a partial quantity of yolk in the sac (especially in the region of the yolk-sac blood capillaries where yolk merocytes abound), it is necessary that the complex colloidal granules be reduced chemically to the simpler crystalloid condition before their diffusion through the yolk-sac wall and those of its blood capillaries actually becomes possible. This change is effected, in all probability, by the yolk-sac blastoderm ('periblast' of teleostean fishes, R. Assheton, 1907) which, in fishes, is known to behave like a trophoblast to the extent that it brings about an *extraembryonic digestion* of the yolk in question. It is, however, reasonable to suppose that only a fractional quantity of the yolk is treated thus and conveyed to the embryonic circulation by diffusion—up to the critical stage of Beard, and that the major quantity of it is conveyed to the embryo, possibly unaltered and more directly along the yolk-duct into its intestine which, presumably along with the other organs of alimentation, has started functioning by that time of the embryonic development.

Balfour (1885) writes that both these modes of food absorption, viz., absorption of the nutritive yolk through foetal blood capillaries and the direct transference of yolk to the embryonic intestine continue simultaneously, whereas Beard (1896) suggests that the former alone exists upto the 'critical stage' and then the latter commences. Beard's suggestion that diffusion through yolk-sac blood-capillaries loses its importance at the 'critical stage' appears reasonable for, when once a direct communication is established between the yolk-sac and the embryonic intestine, the volume of yolk transference is bound to be greater along that direct route than by its indirect transference by the diffusion process. Nevertheless, it may be stated that the latter form of food transference does not dwindle but must actually increase in volume *than before*, for, an examination of the embryos in progressive development stages reveals that the yolk-sac blood capillaries actually increase in size and number

¹ Critical stage is, according to Beard, that stage of embryonic development when the sex of the embryo is defined internally and externally.

with the growth of the embryo, thus affording a greater surface for contact and diffusion.

The stages described above must occur not only in oviparous, ovo-viviparous and aplacental viviparous elasmobranchs but also in placental forms upto the stage at which the placenta is formed. In the latter group, the nutritional process after the formation of the placenta (epithelio-chorial) may be described on the following physiological basis. Simplified nutritive elements in the form of diffusible crystalloids and dissolved gases circulate in the (maternal) blood of the trophonematous villi (just as they do in the maternal blood in mammals) and diffuse through the various placental barriers into the foetal blood, whence they are carried away by the foetal circulation and distributed to the various organs and systems according to their respective needs. On the ground of their advanced anatomical development, it may be held that these organs carry out their own elaboration and synthesis from the requisite simplified elements derived originally from the maternal blood, thus participating actively in the foetal metabolism. Such an explanation of the functional activity of the placenta in this group is only in keeping with the view that a 'true trophoblast' is never developed in fishes as a class and with the observation that it is only formed at a fairly advanced stage of embryonic development which must yet proceed to bring the foetus to term.

Finally, no discussion of the selachian placenta can be regarded as complete without a mention of the 'appendicula'—structures appended to the umbilical cords (later, the placental cords) of placental elasmobranchs. Alcock (1890), to whom we owe their appropriate designation, was the first to describe them on the placental cords of the embryos of *Zygaena blochii* and he considered their probable function to be the absorption of the nutritive secretions of the gravid uterine mucous membrane. Southwell and Prashad (1919) have described four different kinds of appendicula in the elasmobranchs examined by them and they, too, are inclined to attribute to appendicula the same absorptive function as suggested by Alcock.

Being derived from the sheath of the umbilical cord appendicula ultimately bear relationship to the yolk-sac placenta. It is a curious phenomenon that they are not found to develop on the yolk-stalks or umbilical cords of aplacental elasmobranchs. The large quantities of yolk contained in the ova of such aplacental selachoids as *Galeocerdo tigrinus* and *Carcharinus dussumieri* (Mahadevan, 1940), supplemented by the nutritive albuminous secretions of the nidamental glands, suffice, in all probability, to meet the nutritive needs of their embryos throughout their intrauterine life. Hence, the need for the uterine secretions and their absorption by such extraneous structures as appendicula must not arise in them at all. More or less parallel conditions may be said to prevail among the Batoids, which, too, are non-placental. They, too, possess large ova and the yolky food is supplemented in them by the milky nutritive uterine secretions which are poured directly into the pharynx of the developing embryos by the trophonematous villi developed all over the mucous membrane of the gravid uterus. The various foetal and maternal structures in

these elasmobranchs, developed, though temporarily during the emergency, are evidently sufficient in themselves to cope with all this nutritive material and the necessity of appendicula does not arise in them at all.

In the placental elasmobranchs the initial quantity of yolk in the mature ovum and the functional efficiency of the placenta developed appear to be two important factors influencing the production of additional nutritive uterine secretions and consequently, the development or otherwise of the appendicula on the umbilical cords of their embryos. Southwell and Prashad (loc. cit.) have attempted to describe four different grades of appendicular development in the few elasmobranchs examined by them and four corresponding grades of placental evolution in the inverse ratio. On the basis of their observations they conclude: 'In the species with the best developed appendicula, the placenta is of the most primitive and least evolved type and vice versa', thus postulating a regular inverse relationship between appendicular development and placental evolution among elasmobranchs. Evidently they did not take into account that there could be factors other than placental efficiency which could influence the development of appendicula on the cords of the embryos. I cannot, however, help remarking here that this attempt of the authors at thus grading and correlating appendicular development and placental efficiency is purely an empirical one, in view of the facts that not only is the very anatomy of the placentae erroneously described by them, but also that they have not furnished any reasonably acceptable basis for assaying the differential development of the appendicula or the corresponding grades of placental efficiency. Thus, for example, they describe the placentae of *S. sorrakowah* and *S. palasorrah* as being anatomically similar—of the simple contact type, whereas, in point of fact, the placenta of *S. palasorrah* is of the firm inter-digitating type (*vide* Table). They also describe the placenta of *S. walbeehmi* as being of an altogether different type, whereas factually this placenta, as well as that of *S. palasorrah*, is of the same inter-digitating type, representing the epithelio-chorial variety histologically. Further, according to the authors, the appendicula in *S. walbeehmi* and a *Scoliodon* sp. from Ceylon belong to two altogether different grades of anatomical development and yet their placentae are described as belonging to the same grade of evolution—the arborescent type—the type which corresponds to none other than the inter-digitating type of placentae described by me in almost all the placental forms with the exception of *S. sorrakowah*.

Whither then the authors' postulation of a regular inverse relationship between the appendicula and the placentae? While the above-quoted statement of Southwell and Prashad may be said to hold good only in the solitary and extreme case of *S. sorrakowah*, and that, too, only with a certain reserve¹ the converse of the state-

¹ It must be borne in mind that in *S. sorrakowah* the excessive appendicular growth cannot be solely correlated to the very poorly developed placenta, it being equally true that even the initial quantity of the yolk in the mature ovum in this species is a negligible quantity—a factor which must, in part at least, influence the appendicular growth in this form. (*vide* Setna and Sarangdhar—*Rec. Ind. Mus.*—XLVI, Pts. 1-4-1949.)